MORPHOLOGICAL VARIATION IN *MALACOTHAMNUS FASCICULATUS* (TORREY & A. GRAY) E. GREENE (MALVACEAE) AND RELATED SPECIES

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ABSTRACT

Character polymorphism is widespread and species delimitation is unresolved among 11 species of *Malacothamnus* currently recognized in California and Baja California. To evaluate variation among characters used in previous taxonomic treatments and to identify characters most useful for discriminating among four species closely associated with *M. fasciculatus,* we analyzed 26 morphological characters from 46 exemplar specimens using cluster, ordination, and statistical analyses. Although many vegetative and reproductive characters exhibited high levels of variation among and within OTU's, bractlet and calyx characters demonstrated maximum utility for discriminating among species in principal components and discriminant functions analyses. OTU's representing previously segregated "varieties" of *M. fasciculatus* (Torrey & A. Gray) E. Greene did not group together nor did conspecific OTU's, except for three OTU's representing the San Clemente Island endemic, *M. clementinus* (Munz & I. M. Johnston) Kearney. The absence of well-defined gaps in many characters and intergradation resulting from gene flow and/or recent divergence from ancestral species impede delimitation at the species and infraspecific levels whether a phenetic or phylogenetic approach is employed. *Malacothamnus fasciculatus* and *M. fremontii* A. Gray are particularly variable and difficult to define unambiguously using morphological data.

INTRODUCTION

Malacothamnus Greene is a genus of woody or suffrutescent perennials with 11 species currently recognized in California and Baja California (Bates 1963, 1993). Distributed from Mendocino and Tehama Counties in northern California to Rosario, Baja California Norte, species of *Malacothamnus* are primarily associated with chaparral and coastal sage scrub communities. The common names of *Malacothamnus,* chaparral mallow and bush mallow, reflect its habit and habitat preferences.

Established by E. L. Greene (1906), *Malacothamnus* is characterized by uniovulate, unappendaged, completely dehiscent carpels; ascending ovules; and a shrubby habit. Later treatments place *Malacothamnus* in Tribe Malveae, Subtribe Abutilinae (Kearney 1951a, b). Bates (1968) did not recognize subtribes, but regrouped the Malveae into "alliances" and suggested a *Malacothamnus* alliance consisting of *Malacothamnus* (**n** = 17), *Iliamna* Greene (**n** = 33), and *Phymosia* Desvaux (**n** = 17). Based on cytological evidence coupled with inference of Tertiary floristic evolution, Bates (1967, 1968) suggested that the three genera are derived from a *Phymosia*-like ancestor. Eastwood (1939) proposed that the California *Malvastrum* (*Malacothamnus*) was an old genus of previously greater abundance, but now in decline. Kearney (1951b) noted that the lack of pronounced morphological differences among species of *Malacothamnus* suggested a recent origin for the genus.

Although the genus *Malacothamnus* is morphologically distinct within Malvaceae, species and varietal delimitations are problematic because of character intergradation and morphological variation both within and among populations (Kearney 1951b; Bates 1963, 1993). The degree of taxonomic uncertainty and instability is evident when considering the widely fluctuating number of species recognized in different treatments. Whereas Greene (1906) recognized nine species, subsequent treatments recognized from one (Bates 1963) to twenty-seven (Eastwood 1936) species and a variable number of infraspecific taxa. In the most recent treatments of the California species, Kearney (1951b) recognized 19 species and six varieties and Munz and Keck (1968) delimited 18 species, one subspecies, and six varieties. In the Jepson Manual (Hickman 1993), Bates recognized ten species without infraspecific taxa; taxa previously ranked as subspecies (Bates 1963) were elevated to species level without changes in circumscriptions (Bates, personal communication). Skinner et al. (1995) noted that several *Malacothamnus* taxa are of "uncertain distinctiveness" and calculated that 75% of the taxa in the genus are taxonomically uncertain.

Few characters unique to any species have been identified in previous taxonomic treatments. Generally, combinations of overlapping characters have been used to delimit species (Kearney 1951b; Bates 1963, 1993). These recent treatments have employed type and density of calyx pubescence, length and shape of the calyx lobes, length and shape of the bractlets, relative length of the invol-

ucel bractlets and calyx lobes, type of inflorescence, and shape and texture of the leaves (Kearney 1951b; Bates 1963, 1993). For example, *M. fremontii* A. Gray and *M. davidsonii* (Robinson) E. Greene can be identified by thick, often densely pubescent leaf blades, but other species are not easily distinguished based on leaf characters. Bates (1963) provided an example where polymorphism in leaf shape in a single population of about 50 individuals of *M. fasciculatus* (Torrey & A. Gray) E. Greene encompassed almost all the variation found throughout the genus. Differences in habit among species sometimes may be observed, which may result from environmental factors such as water stress, fire, and competition, affecting growth form (Bates 1963).

The basic floral arrangement within *Malacothamnus* is a cyme arranged into terminal heads, spikes, or open panicles (Bates 1963); variation can be found in the length, number of nodes, branching, internode length, and leafiness of the inflorescence (Bates 1963). Examples include *M. densiflorus* (S. Watson) E. Greene, which is distinguished by a densely flowered, spike-like inflorescence with elongate internodes; and *M. palmeri* (S. Watson) E. Greene, which has a densely flowered, head-like or short, spike-like inflorescence subtended by conspicuous bracts (Bates 1993). Involucel bractlet and calyx characters also have been used to delimit species, but exhibit polymorphism within and among species (Kearney 1951b; Bates 1963, 1993). Within *Malacothamnus,* bractlet length ranges from 2.5 to 21 mm and calyx length varies from 5 to 19 mm (Bates 1993). A single species, *M. densiflorus,* encompasses most of the range for these characters; its bractlets vary from 5 to 15 mm in length and its calyces from 6 to 14 mm. Unlike leaf, inflorescence, bractlet, and calyx characters, morphology of the corolla, pistil, stamen, carpels, and seeds provide few characters used to segregate species (Kearney 1951b; Bates 1963).

Similar to problems in species delimitation and identification, infraspecific taxa in *M. fasciculatus* are notoriously difficult to identify. Although extreme morphological forms are evident, intergradation among habit, leaf shape and pubescence, inflorescence structure, and carpel characters is widespread. Five varieties of *M. fasciculatus* were described previously by Kearney (1951b) and eight subspecies by Bates (1963) in an unpublished dissertation. Later, Bates (1993) recognized no infraspecific taxa in *M. fasciculatus.* In a study of molecular variation in *M. fasciculatus,* Swensen et al. (1995) provided data that indicated var. *nesioticus* is genetically distinct from other varieties of *M. fasciculatus.*

We conducted this study to initiate analyses of character variation within and among species of *Malacothamnus.* Although previous taxonomic and floristic treatments (Kearney 1951b; Bates 1963) emphasized the lack of constant, unique characters

and the high level of variability found within species, there have been no explicit numerical studies of the amount and pattern of variation nor statistical analyses of characters that differentiate species. *Malacothamnus fasciculatus* is morphologically and geographically diverse, has been examined at the molecular level (Swensen et al. 1995), and intergrades commonly with other sympatric species, particularly in the southern portion of its range. The present study focused on variation in morphological characters among five intergrading species: *M. clementinus* (Munz & I. M. Johnston) Kearney, *M. davidsonii, M. densiflorus, M. fasciculatus,* and *M. fremontii.* The primary objectives of the study were to assess variation among characters used in previous taxonomic treatments, to identify characters that discriminate among species, and to test hypotheses of taxonomic delimitation of species and varieties.

The five species examined in this study are widespread in southern California and Baja California Norte, and one species is distributed in northern as well as southern California. *Malacothamnus fasciculatus* as delimited by Kearney (1951b) ranges from Santa Barbara County to Baja California Norte. Kearney (1951b) recognized five varieties: vars. *fasciculatus* Greene, *laxiflorus* (Gray) Kearney, and *nuttallii* (Abrams) Kearney are restricted to mainland California, whereas var. *catalinensis* (Eastw.) Kearney (found on Santa Catalina Island and coastal Ventura to San Diego Counties) and var. *nesioticus* (B. L. Rob.) Kearney (restricted to Santa Cruz Island) have populations on the California Islands. Also widely distributed are *M. fremontii,* ranging from Tehama to Riverside Counties and *M. densiflorus,* which is distributed from Riverside County to northern Baja California Norte. The federally and state listed endangered species *M. clementinus* (Smith & Berg 1988) is endemic to San Clemente Island. Populations of *M. davidsonii* are separated by the Transverse Ranges between Los Angeles County and San Luis Obispo and Monterey Counties.

MATERIALS AND METHODS

We examined variation among 26 morphological characters among five species of *Malacothamnus* using clustering, ordination, and statistical analyses. Taxonomic identity was determined using keys and descriptions from the Jepson Manual (Hickman 1993) and, for "varieties" of *M. fasciculatus,* Kearney's treatment (1951b) and Munz and Keck (1968) were used. One representative individual from each of 46 collections representing natural populations (Table 1, Fig. 1) was selected as an exemplar operational taxonomic unit (OTU). The OTU's were chosen from herbarium specimens or from collections of the first author; they were selected to span the geographic and morphological range of each species analyzed (Fig. 1). The widespread species

TABLE 1. SPECIMENS REPRESENTING NUMBERED OTU'S OF FIVE SPECIES OF *MALACOTHAMNUS* USED IN INVESTIGATIONS OF MORPHOLOGICAL VARIATION. All locations are in the state of California unless otherwise noted.

M. clementinus (Munz & Johnston) Kearney

13. San Bernardino Co., Victorville, North Verde Ranch, *Raven 16625*, CAS. 14. Los Angeles Co., San Clemente Island, Lemon Tank, *Beauchamp & Douglas 3236*, SD. 15. Los Angeles Co., San Clemente Island, China Canyon, *Moran, Beauchamp, & Oberbauer 22697*, UC.

M. davidsonii (B. L. Rob.) Greene

11. San Luis Obispo Co., Bee Rock, *Hardham s.n.*, CAS. 12. Los Angeles Co., San Fernando Wash, *Davidson s.n.*, CAS. 16. Los Angeles Co., Big Tujunga, *Lyon s.n.*, CAS. 17. Monterey Co., Lake San Antonio, *Jensen 45*, UC.

M. densiflorus (S. Watson) Greene

9. Mexico, Baja, Valle Redondo, *Fosberg 8368*, UC. 10. Riverside Co., Santa Ana Mtns., above Glen Ivy, *Howell 1056*, UC. 18. San Diego Co., Barrett Lake, *Benesh & Anderson 35*, OKL. 39. San Diego Co., Ramona, *Brandegee s.n.*, UC. 46. Mexico, Baja, San Pedro Martir Mtn., *Robertson 55*, UC.

M. fasciculatus (Nutt. ex Torr. & Gray) Greene

"*var. catalinensis* (Eastwood) Kearney"

5. Los Angeles Co., Santa Catalina Island, Middle Ranch Dam, *Fosberg 54770*, UC. 6. Orange Co., Laguna, *Peirson 4662*, SD. 19. Los Angeles Co., Santa Catalina Island; Black Jack Mtn., *Thorne 36518*, SBBG. 21. Ventura Co., Santa Monica Mtns. beyond Hidden Valley on Sherwood Rd., *Holbrook s.n.*, SBBG.

"*var. fasciculatus* (Nutt. *ex* Torr. & Gray) Greene"

20. San Diego Co., 2 mi E of San Ysidro on Otay Mesa, *Gander 219.13*, SD. 31. Riverside Co., El Toro Peak, San Jacinto Mtns., Santa Rosa Range, *Hall 765*, UC. 32. San Diego Co., Fallbrook; ca. 6 mi NE, *Benesh & Anderson 39*, OKL. 33. Mexico, Baja, Punta Banda near Arbolitos, *Thorne & Charlton 58685*, RSA. 34. Mexico, Baja, Rancho Estela, *Moran 24380*, SD. 35. Mexico, Baja, El Condor, Sierra Juarez, *Moran 13578*, SD. 37. San Mateo Co., Spring Valley, *Cougdon s.n.*, JEPS. 40. Mexico, Baja, Upper Arroyo Copal, Sierra San Pedro Martir, *Moran 15499*, SD. 41. Mexico, Baja, Santa Rosa, *Moran & Thorne 14427*, RSA. 44. San Bernardino Co., San Bernardino Mtns., State Hwy 18 ca 0.5 mi above Waterman Canyon Road, *Raven & Beeks 16759*, UC. 45. Mexico, Baja, Socorro Wash (Arroyo Hondo), *Thorne, Wisura, Peterson, & Annable 58011*, RSA.

"*var. laxiflorus* (Gray) Kearney"

22. Los Angeles Co., Altadena, *Ramsey & Ramsey 3084*, RSA. 23. Orange Co., Crystal Cove State Park, El Moro Canyon, *Benesh 57*, OKL. 24. San Bernardino Co., Cajon Pass, *Benesh 53*, OKL. 27. Ventura Co., Point Mugu, *Vanderwier & Murphey 78*, SBBG. 30. Riverside Co., Garner Valley, *Tilforth & Wisura 1916*, RSA. 36. San Diego Co., Camp Pendleton, Horno Canyon, *Beauchamp & Swickard 1518*, SD.

"*var. nesioticus* (B. L. Rob.) Greene"

7. Santa Barbara Co., Santa Cruz Island, *Brandegee 1888*, UC.

TABLE 1. (CONTINUED).

"*var. nuttallii* (Abrams) Kearney"

3. Santa Barbara Co., upper Cachuma Dam area, *Smith 4940*, SBBG. 4. Los Angeles Co., Santa Monica Mountains, *Howe 2164*, SD. 25. Santa Barbara Co., Santa Barbara, *Benesh 63*, OKL. 26. Ventura Co., Lake Casitas, near East Casitas Pass, *Benesh 64*, OKL. 43. Santa Barbara Co., Gaviota Pass, *Abrams 5030*, UC.

M. fremontii (Torr. ex Gray) Torr. ex Greene

1. Santa Barbara Co., Vandenburg AFB, *Nichols 664*, JEP. 2. Sutter Co., North Butte, *Ewan & Ewan 9597*, JEP. 8. Madera Co., Oakhurst, *Wolf 2433*, SBBG. 28. Los Angeles Co., Pine Canyon, *Hoffman s.n.*, SBBG. 29. Ventura Co., Lockwood Valley, *unknown s.n.*, SBBG. 38. San Bernardino Co., Baldwin Lake, *Tilforth & Wisura 2107*, RSA. 42. Riverside Co., San Jacinto Mtn., *Purer 6472*, CAS.

M. fasciculatus and *M. fremontii* were disproportionately represented in their southern range where they and other species are sympatric.

Eleven quantitative and 15 qualitative characters were chosen to represent vegetative and reproductive structures (Table 2). Characters were selected based on their inclusion as diagnostic features in previous taxonomic treatments (Kearney 1951b; Munz and Keck 1968; Bates 1963, 1993). For each OTU, we obtained a minimum of 10 measurements for each character whenever possible. Several measurements of bractlet, calyx, and leaf length and/or width were converted to a ratio (characters 2, 7, 17, 18; Table 2) to describe shape and relative dimensions rather than absolute size. Lack of sufficient suitable material on herbarium specimens precluded the use of leaf size, carpel characters, and seed characters in our analysis. Preliminary analyses also revealed that several characters not included in our analysis were either variable on a single individual, too subjective to be coded accurately, or difficult to detect (e.g., leaf lobing, leaf margin, leaf apex, leaf thickness, pubescence color, inflorescence type, and bractlet shape).

Analyses were performed using NTSYS-pc (Rohlf 1993) and SYSTAT (SPSS Inc. 1997). A standardized data matrix was used to compute a dissimilarity matrix using the average taxonomic distance coefficient and a cophenetic correlation coefficient. A clustering phenogram was generated using the UPGMA (unweighted pair-group method using arithmetic averages) method. A Principal Components Analysis (PCA) was performed by computing a correlation matrix, calculating eigenvectors for the first three axes, and projecting the OTU's onto the components.

Using the SYSTAT software package (SPSS Inc. 1997), discriminant functions analysis was used to determine which combination of characters provided maximum discrimination among recognized species and "varieties" of *M. fasciculatus*. Because this method does not allow missing data, seven of
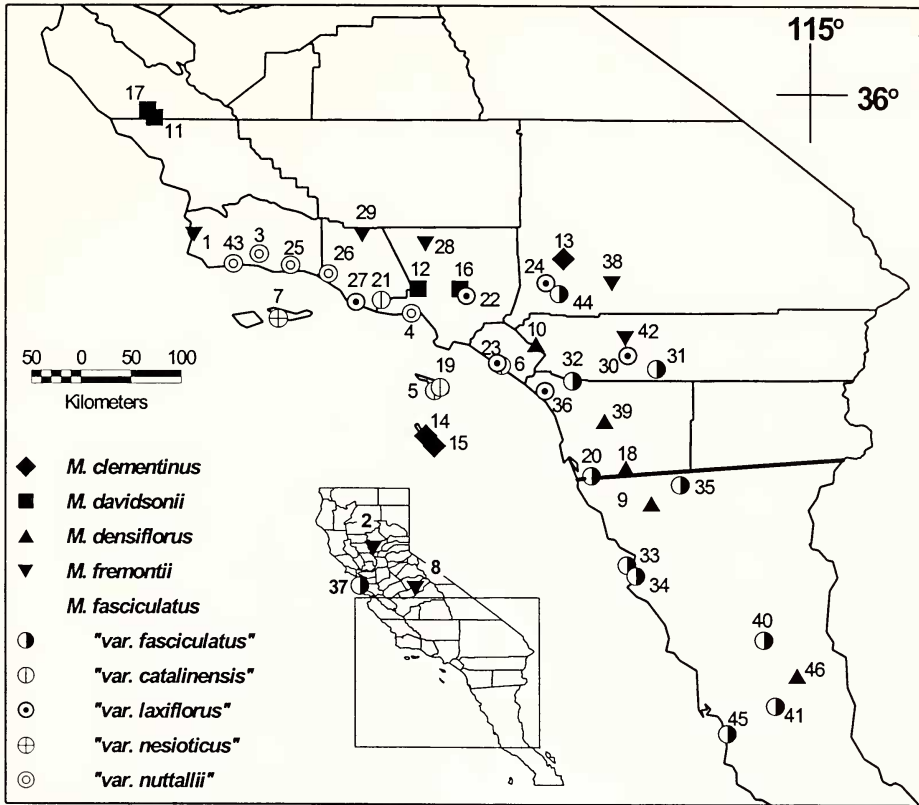
FIG. 1.   Collection localities for 46 specimens of five species of *Malacothamnus* analyzed for morphological variation. Solid symbols represent species described in The Jepson Manual (Hickman 1993; Bates 1993). Shaded symbols represent "varieties" of *M. fasciculatus* as delimited by Kearney (1951b; Munz & Keck 1968).

1288 entries (0.54%) from the data matrix were estimated by using the average of other OTU's of the same species. Standard and jackknifed classifications were produced to test group relationships. In the standard procedure, the centroid of each group of like taxa was computed, and then each OTU was examined to determine to which group it was most similar. When the OTU was most similar to the group representing that taxon, it was scored as a correct identification. When it was most similar to a group representing another taxon, it was scored as an incorrect classification. For the jackknifed classification, an OTU was removed, the centroid recalculated, and the OTU identified as to which group it was most similar. This was repeated for each OTU, producing a less biased number of correct classifications. Three discriminant functions analyses were performed: species level only, species and all "varieties" of *M. fasciculatus,* and species and "varieties" of *M. fasciculatus* except "var. nesioticus". The latter analysis was performed because "var. nesioticus" was represented by only a single OTU, which confounded the jackknifed classification.

RESULTS

The UPGMA phenogram (Fig. 2) had four major clusters and a cophenetic correlation value of 0.840. Cluster I was composed of two OTU's of *M. fremontii* and an OTU representing *M. fasciculatus* "var. *fasciculatus*" of unusual appearance from the southern limits of its range in Baja California Norte. Cluster II was the most complex grouping in the phenogram, and could be further subdivided into three groups, excluding the outlying "var. *fasciculatus*" (OTU 37) from San Mateo County. With the two aforementioned exceptions, all other OTU's representing *M. fasciculatus* were found within cluster II along with OTU's of three other species. Cluster IIa consisted of 10 OTU's representing *M. fremontii, M. davidsonii,* and three "varieties" of *M. fasciculatus.* The closest phenetic similarity among all OTU's was in this cluster between *M. davidsonii* and *M. fasciculatus* "var. *laxiflorus*" (OTU's 17 and 24). Cluster IIb comprised OTU's representing all five "varieties" of *M. fasciculatus* as well as one OTU of *M. davidsonii* from Los Angeles County. The OTU representing the Santa Cruz Island endemic *M. fasciculatus* "var. *nesioti-*

TABLE 2. MORPHOLOGICAL CHARACTERS EXAMINED AMONG FIVE SPECIES OF *MALACOTHAMNUS* AND PURPORTED VARIETIES OF *M. FASCICULATUS*. Characters useful for differentiating among species in principal components analysis (PCA) are indicated by an asterisk (*). Characters useful for differentiating species in discriminant functions analysis are indicated by a plus sign (+).

	1.	stem pubescence type: loose (0), appressed (1)
	2.	leaf blade length/width
	3.	leaf base: cordate (0), truncate (1)
* +	4.	bractlet length
*	5.	bractlets concolorous throughout: absent (0), present (1)
*	6.	bractlet concolorous with calyx: absent (0), present (1)
* +	7.	bractlet length/calyx length
	8.	calyx length from base to tip of lobe
*	9.	calyx outer pubescence type: rigid (0), soft or pliant (1)
* + 10.	10.	sepal lobes in bud recurved at margins: absent (0), present (1)
*	11.	sepal lobes in bud: divergent (0), connivent (1)
	12.	sepal lobe shape: triangular (0), ovate (1)
	13.	sepal lobe apex: acute (0), acuminate (1)
*	14.	sepal lobe constricted at base: absent (0), present (1)
*	15.	sepal lobe length
	16.	sepal lobe width at base
	17.	sepal length/width
	18.	sepal lobe length/calyx tube length
	19.	sepal lobes obscured by pubescence: absent (0), present (1)
+ 20.	20.	sepal pubescence: short-stalked (0), long-stalked (1)
	21.	sepal pubescence: number of arms
*	22.	sepal pubescence: length of arms
	23.	sepal lobe pubescence type within: glabrous (0), tomentose (1), pilose (2), hispid (3)
	24.	inflorescence: unbranched (0), branched (1)
	25.	flower clusters: dense (0), open (1)
	26.	length of staminal column

cus" clustered most closely with "var. *nuttallii*" from Los Angeles County, whereas OTU's of "var. *catalinensis*", including two from Santa Catalina Island, did not group together.

Only *M. densiflorus* and *M. fasciculatus* OTU's were contained in Cluster IIc, which included specimens from south-central Riverside County to the southern limits of the North American range in Baja California. Cluster III was composed of two subclusters of OTU's representing *M. fremontii* and *M. clementinus*. The *M. clementinus* OTU's included a (cultivated?) specimen from San Bernardino County. Cluster IV comprised two *M. densiflorus* OTU's that are less similar to each other than are most of the other clusters.

The three-dimensional PCA model (Fig. 3) revealed groupings similar to those in the UPGMA phenogram. The first three components constituted 49 percent of the total variation: 28%, 11%, and 10%, respectively. Characters with high loadings (Table 3) included characters 4, 7, 11, 15, and 22 in the first component; 9, 10, and 14 in the second component; and 5 and 6 in the third component. The PCA model also did not reveal discrete groupings corresponding to species boundaries, but instead depicted loose groups with considerable overlap among taxa. OTU's representing *M. clementinus, M. densiflorus,* and *M. fremontii* were generally separated from *M. fasciculatus* and *M. davidsonii* along the first axis. There were no discrete groupings among OTU's corresponding to varieties of *M.*

fasciculatus. As in the UPGMA phenogram, the PCA model placed *M. davidsonii* within the *M. fasciculatus* complex.

Discriminant functions analysis identified four characters as most useful for classifying species: 4, 7, 10, and 20 (Table 2). The OTU's were correctly classified to species an average of 67% (Table 4) in the standard classification. Whereas *M. densiflorus* was classified correctly 100% of the time, the lowest value, 56%, resulted when 12 *M. fasciculatus* OTU's were misclassified as *M. davidsonii* (10) or *M. densiflorus* (2). In the jackknifed classification, a 52% average correct classification was obtained. The lowest value, 44%, resulted when 15 OTU's of *M. fasciculatus* were incorrectly classified.

When "varieties" of *M. fasciculatus* were included as taxa, characters 7 and 10 (Table 2) were the most useful for discriminating among species and "varieties" using discriminant functions analysis. The correct classification percentages were relatively unchanged by the exclusion of the one OTU of "var. *nesioticus*". The standard classification was correct 43% of the time when "var. *nesioticus*" was included (Table 4) and 47% when it was removed compared to jackknifed percentages of 35% when "var. *nesioticus*" was included and 36% when it was excluded. *Malacothamnus davidsonii* and *M. fasciculatus* "var. *laxiflorus*" were consistently classified incorrectly in analyses including varieties. For example, OTU's of *M. dav-*
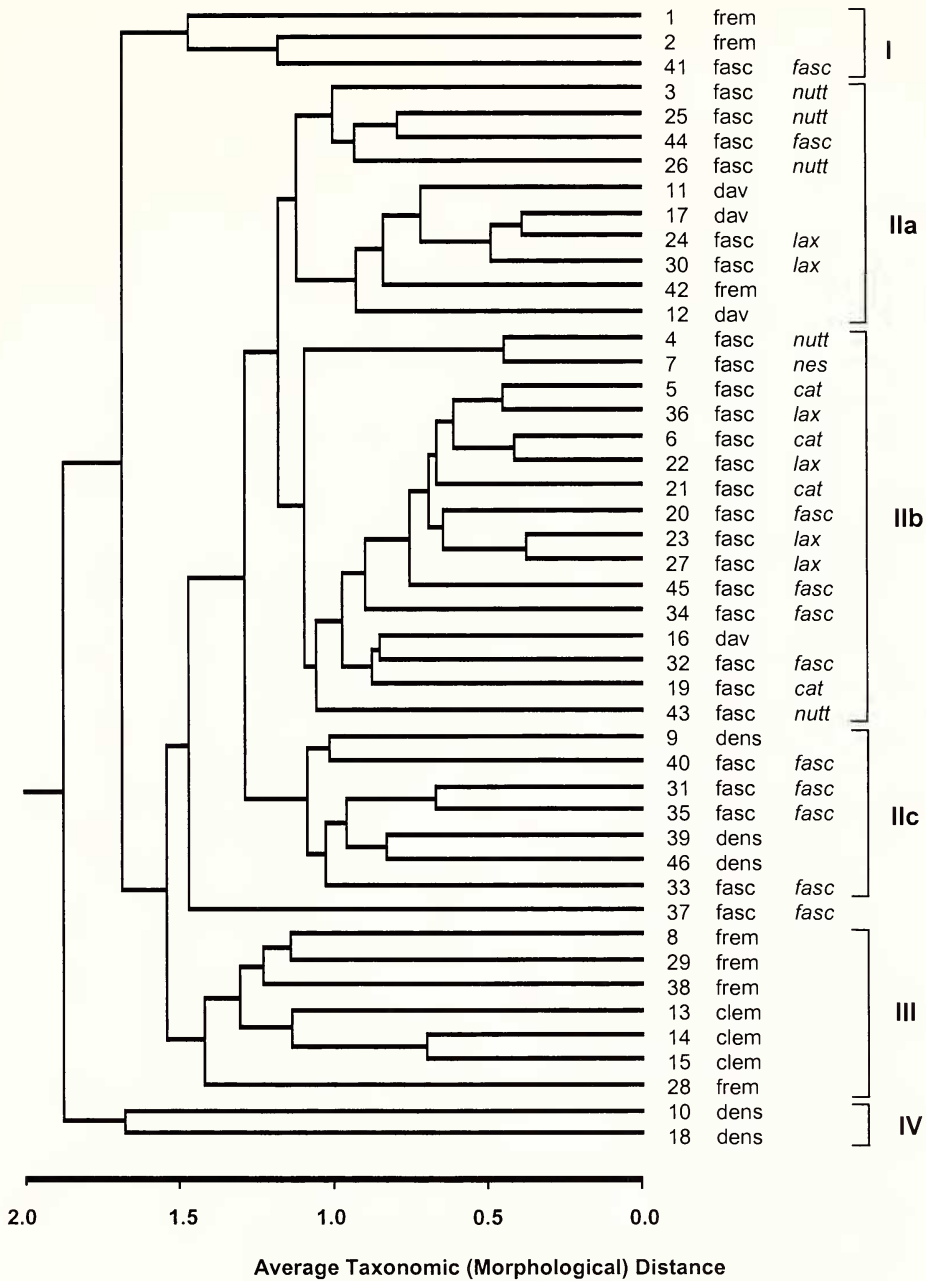
Fig. 2.   UPGMA phenogram derived from average taxonomic distance coefficients using 26 morphological characters from 46 OTU's of five species of *Malacothamnus*. OTU numbers and locations are listed in Table 1. The cophenetic correlation is 0.840.

idsonii were classified as "var. *nesioticus*", "var. *nuttallii*" or "var. *laxiflorus*".

DISCUSSION

Character variation and life history traits. The diverse taxonomic interpretations within *Malacothamnus* reflect complex patterns of morphological variation. Our observations and analyses confirm that many characters used previously exhibited high levels of variability within species, populations, and, even, single individuals. This point often was commented upon to varying degrees by previous workers (Kearney 1951b; Bates 1963, 1993), but there has been no quantification or documentation of character variation until the present study. We found that most vegetative characters used previously to delimit and characterize species, particularly those describing the vestiture, lobing, apex,
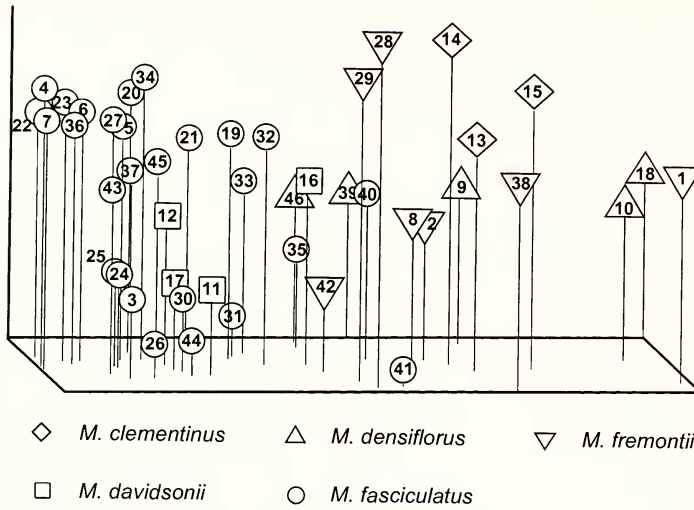
FIG. 3. Three-dimensional model produced in principal components analysis using 26 morphological characters in five species of *Malacothamnus*. OTU numbers and locations are listed in Table 1.

and margins of leaves, were too variable on specimens to code or to describe accurately the phenotype of a collection or OTU. Our study is at least partially supportive of Bates' (1963) comment that some characters are vague or difficult to quantify, but are apparent to those familiar with the genus. This was particularly noteworthy for *M. davidsonii*, whose "coarse" habit, "stout" branches, and "densely" pubescent leaves are readily observable in field populations, but difficult to observe and quantify on herbarium specimens. Consequently, only one stem and two leaf characters were included in the analyses out of 26 total characters. Of the three vegetative characters identified, none were indicated as "useful" for discriminating among species in our analyses.

Reproductive characters, especially those de-

TABLE 3. EIGENVALUES PRODUCED IN PCA FOR 26 MORPHOLOGICAL CHARACTERS AMONG FIVE SPECIES OF *MALACOTHAMNUS*. Character numbers refer to Table 2.

Character	Component 1	Component 2	Component 3
1	−0.185	−0.233	0.361
2	−0.070	0.235	0.059
3	0.019	0.248	−0.458
4	0.899	0.168	0.117
5	0.490	−0.068	−0.632
6	0.256	0.129	−0.750
7	0.802	0.343	0.244
8	0.678	−0.320	−0.223
9	0.426	−0.496	−0.020
10	−0.630	0.483	−0.422
11	−0.780	0.231	−0.370
12	−0.040	0.303	0.177
13	0.012	0.416	0.088
14	0.433	0.563	−0.239
15	0.788	−0.308	−0.327
16	0.152	−0.215	−0.210
17	0.713	−0.287	−0.324
18	0.681	−0.228	−0.332
19	−0.563	−0.395	−0.146
20	0.480	−0.418	0.388
21	−0.524	−0.365	−0.365
22	0.760	0.308	0.217
23	0.092	0.305	−0.273
24	−0.489	−0.436	−0.191
25	−0.500	−0.385	−0.060
26	0.125	−0.211	0.086

TABLE 4. PERCENTAGE OF TAXA CORRECTLY CLASSIFIED IN DISCRIMINANT FUNCTIONS ANALYSIS OF 26 MORPHOLOGICAL CHARACTERS AMONG FIVE SPECIES OF *MALACOTHAMNUS*. Results are presented for comparisons among species only and among species and all "varieties" of *M. fasciculatus*. See text for discussion of results when "var. *nesioticus*" was removed from the analysis.

	Percent correctly classified			
	Species only		Including "varieties" of *M. fasciculatus*	
Taxa	Standard	Jack-knifed	Standard	Jack-knifed
M. clementinus	67	67	100	67
M. davidsonii	75	50	0	0
M. densiflorus	100	60	80	80
M. fremontii	86	71	29	29
M. fasciculatus	56	44	—	—
"var. *catalinensis*"	—	—	75	75
"var. *fasciculatus*"	—	—	45	36
"var. *laxiflorus*"	—	—	0	0
"var. *nesioticus*"	—	—	100	0
"var. *nuttallii*"	—	—	40	20
Total	67	52	43	35

scribing the bractlets and calyx, were more consistent within OTU's, were easier to code, made up the majority of characters subjected to numerical analyses, and comprised all 11 characters that discriminated most effectively among species in the PCA and/or discriminant functions analyses (Table 2). Other reproductive characters describing the inflorescence and staminal column exhibited little utility for discriminating among species. Three characters exhibited high levels of discrimination among species in both PCA and discriminant functions analyses, and represent characters of maximum taxonomic utility: bractlet length, bractlet length/calyx length, and the presence or absence of recurving sepal lobe margins in bud. Another five qualitative and three quantitative characters were significant in either PCA or discriminant functions analyses: bractlets concolorous with calyx, bractlets concolorous throughout, outer calyx pubescence texture, divergence of sepal lobes in bud, sepal lobe constriction at base, sepal lobe length, and length of the arms and stalks of the sepal pubescence.

Variation patterns observed among species reflect historical factors such as biogeography and phylogeny, and genetic factors such as population structure, mating system, reproductive isolation, and seed dispersal (Avise 1994). Populations of *M. fasciculatus* and related species vary in size from few to numerous individuals, consist often of clones because of reproduction via rhizomes (Bates 1963; Swensen et al. 1995), and are characterized by lack of fertility barriers (Bates 1963). Artificial hybridization experiments revealed widespread cross-compatibilities and interfertilities among species (Bates 1963). Natural hybridization between species also has been postulated; Bates (1963) identified four regions of sympatry with interspecific hybrid swarms. Bates (1963) suggested that "random but recurrent hybridization and isolation of populations has probably been a major factor in the evolution of morphological diversity in *Malacothamnus*."

Variable compatibility systems may be present among species of *Malacothamnus*; *M. fasciculatus* and *M. palmeri* are self-incompatible, whereas self-compatibility has been observed in *M. fremontii* and *M. jonesii* (Bates 1963). Additionally, Bates (1963) observed that although the flowers of *Malacothamnus* are bisexual and pollen is released while stigmas are receptive, insects commonly visit the flowers. He concluded that species of *Malacothamnus* have a mixed mating system but are predominantly outcrossing. However, in an examination of genetic variation within *M. fasciculatus,* Swensen et al. (1995) reported a value of isozyme differentiation among ten populations ($G_{st} = 0.584$) which is most concordant with that of a selfing species (Loveless and Hamrick 1984; Hamrick and Godt 1990). Because of the lack of interspecific reproductive barriers, gene flow among populations and species may be partly responsible for character

intergradation in *Malacothamnus* (Loveless and Hamrick 1984; Briggs and Walters 1985). Additionally, replenishment of alleles from the soil seed bank may contribute to heterogeneity within and among populations (Huenneke 1991). Germination experiments indicate that *Malacothamnus* seeds remain viable for more than 50 years (Bates 1963; Benesh unpublished data) and germinate rapidly following a fire (Bates 1963).

Taxonomic implications and species delimitation. Among 46 OTU's included in clustering and ordination analyses, only those representing *M. clementinus* formed a distinct cluster and grouped with OTU's of *M. fremontii.* Sampled specimens of other species were intermixed in the UPGMA phenogram and PCA model. *Malacothamnus fasciculatus* was the most widely sampled species and encompassed the most morphological variation. Similar to the interspecific pattern, OTU's representing segregated "varieties" of *M. fasciculatus* were completely intermixed and clustered with those of three other species: *M. fremontii, M. davidsonii,* and *M. densiflorus.* The 16 specimens in cluster IIb of the phenogram (Fig. 2) formed the most internally consistent taxonomic grouping, with one *M. davidsonii* in a group of *M. fasciculatus* OTU's.

The general lack of resolution delimiting species of *Malacothamnus* using numerous characters and a phenetic approach indicate polymorphism among species was extensive. In our study, multivariate techniques did not identify any well-defined morphological and geographic cluster within *Malacothamnus.* The pattern of morphological and geographical variation was widespread among the five species sampled, and character intergradation was not restricted to particular species pairs or to a few areas of sympatry. Conspecific OTU's were generally spatially separated on the phenogram (e.g., OTU's 16+32+19 and OTU's 17+24+30), except for cluster IIc where three *M. densiflorus* specimens grouped with four OTU's of *M. fasciculatus* in an area of sympatry and purported hybridization (Bates 1963). Although found at elevations less than 650 meters throughout much of its range (Bates 1963), inland populations of *M. fasciculatus* in Riverside and San Diego Counties and northern Baja California Norte can be found at higher elevations, resulting in sympatry with *M. densiflorus* (Fig. 4). Bates (1963) recognized this area as a zone of introgression and suggested that delimitation of *M. densiflorus* and *M. fasciculatus* is arbitrary in this region.

Because comparatively few characters exhibited significant taxonomic utility (Table 2), it is useful to consider whether a phylogenetic approach to species delimitation (e.g., Nixon and Wheeler 1990, Davis and Nixon 1992), based on uniform and unique characters or combinations of characters, is more useful than the phenetic methods used in this study. Population (OTU)-based data have been used
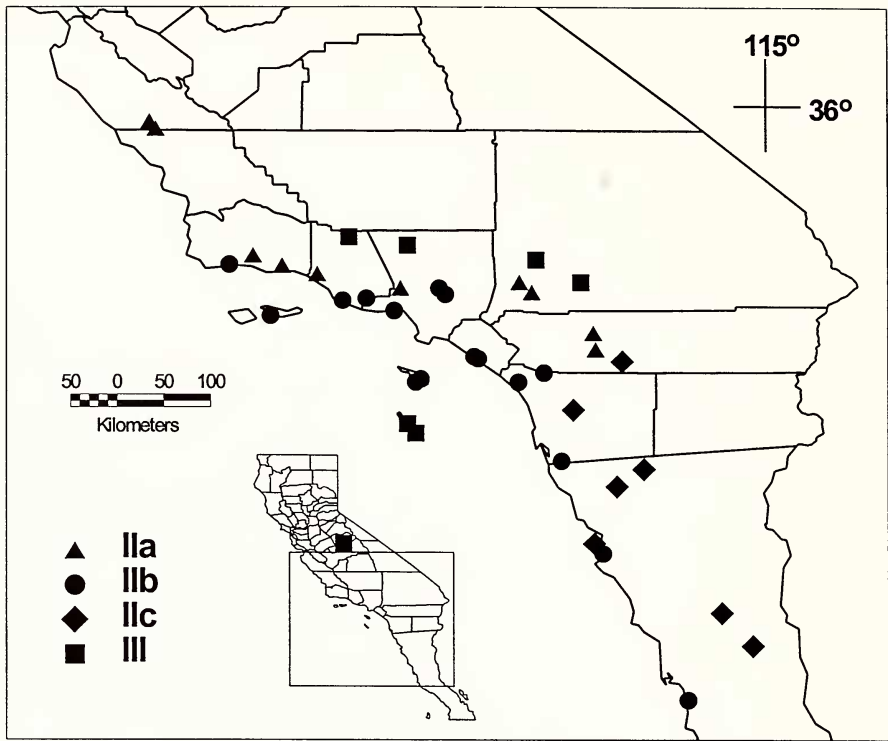
Fig. 4. Collection locations for specimens of five species of *Malacothamnus* analyzed for morphological variation. Cluster designations correspond to the clusters produced in the UPGMA phenogram (Fig. 2). Only clusters II and III are shown.

successfully to identify lineage-defining characters in several groups (e.g., Davis and Manos 1991), and several species of *Malacothamnus* can be delimited using morphological data with this procedure. For example, *M. densiflorus* can be defined by a unique character combination of an unbranched, elongated inflorescence, dense flower clusters, and large bractlet and calyx lengths. *Malacothamnus clementinus* is identified by the association of isodiametric leaves (similar to *M. fasciculatus*) and recurved sepal lobes in bud (similar to *M. fremontii*). The combination of "stout" branches and "dense" leaf pubescence of *M. davidsonii* also are unique in the genus and are used to define this species by several workers (Kearney 1951b; Bates 1963, 1993). However, in *M. davidsonii* as in *M. fasciculatus, M. fremontii,* and other species in *Malacothamnus,* lineage-defining characters are often difficult to detect in herbarium specimens, vary greatly among and within populations, and are difficult to divide into discrete character states. The absence of well-defined gaps in many characters and intergradation resulting from gene flow and/or recent divergence from ancestral species pose serious problems to species delimitation within *Malacothamnus* whether a phenetic or phylogenetic approach is employed.

Malacothamnus fasciculatus and *M. fremontii*

encompass the largest geographical range and morphological variation among the species investigated and in the genus (Bates 1963). Illustrating the discordant views of species boundaries and the extent of phenotypic variation among these species, Bates (1993) submerged five and three specific epithets to synonymy within *M. fasciculatus* and *M. fremontii,* respectively. Other than geographic locality (e.g., "var. *catalinensis*", "var. *nesioticus*"), varieties of *M. fasciculatus* were equally difficult to characterize and were not recognized in the Jepson Manual (Hickman 1993). Because of complex patterns of intergradation among morphological characters, we were not able to identify any unique character combinations for *M. fasciculatus* or *M. fremontii.*

Using molecular data, Swensen et al. (1995) examined variation among varieties of *M. fasciculatus* to assess the genetic distinctness of the two known populations of the Santa Cruz Island endemic, *M. fasciculatus* "var. *nesioticus*". Sampling within *M. fasciculatus* was from six counties and was based on ten populations in the isozyme studies and seven populations in the RAPD and rDNA analyses. Swensen et al. (1995) concluded that the pattern of molecular variation supported Kearney's (1951b) varietal delimitations within *M. fasciculatus,* and that "var. *nesioticus*" was the most divergent ge-

netically among sampled populations with unique isozyme and RAPD alleles and rDNA restriction sites. Our morphological analyses indicate a conclusion similar to Bates (1963, 1993) is warranted. There is extensive morphological intergradation among "varieties" of *M. fasciculatus* and we are unable to characterize any variety unambiguously, including "var. *nesioticus.*"

Biogeographic implications. Populations of two species examined in this study, *M. fasciculatus* and *M. clementinus,* are considered California Island endemics or island-mainland disjuncts. Whereas *M. clementinus* is restricted to San Clemente Island, previously segregated "varieties" of *M. fasciculatus* included a Santa Cruz Island endemic ("var. *nesioticus*") and a Santa Catalina Island and mainland disjunct ("var. *catalinensis*"). Our results supported the status of the endangered species *M. clementinus* as a distinct morphotype in *Malacothamnus* that may be found occurring naturally only on San Clemente Island. *Malacothamnus clementinus* forms the most morphologically coherent group for any species examined, and its three OTU's are most similar morphologically to four OTU's of *M. fremontii* collected at elevations ranging from 1160 to 1500 meters in Los Angeles, Madera, San Bernardino, and Ventura Counties. Our analyses included an OTU (P. H. Raven #16625, annotated by Bates) from San Bernardino County, but it was unclear if it was a human-facilitated introduction. Bates (1963, 1993) previously noted the similarities between *M. clementinus* and *M. fremontii* in calyx characters, and suggested that *M. clementinus* represented a "generalized" form of *Malacothamnus* that persisted in refugial habitats in San Clemente Island (Raven and Axelrod 1978).

Mainland and island OTU's representing *M. fasciculatus* "var. *catalinensis*" did not group together in our morphological analyses, indicating polymorphism among Santa Catalina Island and mainland populations formerly placed in "var. *catalinensis*". We present no morphological evidence to characterize "var. *catalinensis*" or to support its status as a California Island endemic or island-mainland disjunct. For *M. fasciculatus* "var. *nesioticus*", its coherence as a distinctive morphotype within *M. fasciculatus* and as a Santa Cruz Island endemic could not be tested because only one OTU was examined. Swensen et al. (1993) found that the two known populations of "var. *nesioticus*" were more dissimilar genetically to each other than either population was to other "varieties". Our PCA indicated that the Santa Cruz Island OTU was most similar to a collection of *M. fasciculatus* "var. *nuttallii*" from the Santa Monica Mountains in Los Angeles county. This morphological grouping is geographically proximate and also is consistent with the hypothesized physiographic and geological correspondence of the northern California Islands with the western

Transverse Ranges (Valentine and Lipps 1967, Sorlien 1994).

The rare species *M. davidsonii* is disjunct between the South Coast Ranges and Los Angeles County. The four OTU's representing these disjunct regions did not group together, but exhibited the closest morphological similarity to *M. fasciculatus* and, to a lesser extent, *M. fremontii.* Our data support Bates' (1963, 1993) observation of the intergradation between *M. davidsonii* with *M. fasciculatus.* As in this and other examples of character intergradation between species, this study cannot differentiate between hypotheses of interspecific hybridization or primary (and incomplete) divergence from ancestral species. Future studies employing molecular markers may represent the best approach to investigate specific instances of gene flow, species delimitations, and interspecific relationships.

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